Towards a taxonomic revision of *Pteridium* (Dennstaedtiaceae)

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Abstract

Thomson, J.A. (National Herbarium of NSW, Royal Botanic Gardens and Domain Trust, Sydney, NSW 2000, Australia) 2004. Towards a taxonomic revision of Pteridium (Dennstaedtiaceae). Telopea 10(4): 793–803. Controversy concerning typification of the bracken fern Pteridium aquilinum (L.) Kuhn is here resolved and an epitype proposed. Bracken taxa recognised in current European and Asian regional floras can for both land masses be placed in two morphologically and genomically distinct groups: an 'aquilinum' group and a 'latiusculum' group. Limited, presumably ongoing, gene flow between 'aquilinum' and 'latiusculum' morphotypes is attested in field situations of sympatry or parapatry by the presence of stands of intermediate morphotype, and by DNA fingerprinting. In Europe, 'aquilinum' morphotypes are referable to P. aquilinum subsp. aquilinum; in Asia, to P. aquilinum subsp. wightianum (Wall. ex J. Agardh) Shieh. To facilitate consistent, objective systematic treatment of 'latiusculum' morphotypes in Europe and Asia, P. aquilinum subsp. latiusculum (Desv.) Hultén is redefined to include only specimens from the North American region, and paratypes designated. Similar morphotypes from Europe are referred to P. aquilinum subsp. pinetorum (C.N. Page & R.R. Mill) J. A. Thomson, and those from north-east Asia are referred to *P. aquilinum* subsp. *japonicum* (Nakai) Á. Löve & D. Löve for which a lectotype is chosen and syntypes identified. The endemic Hawaiian bracken morphotype is here formally recognised at subspecies rank as P. aquilinum subsp. decompositum (Gaudich.) Lamoureux ex J.A. Thomson.

Introduction

The cosmopolitan bracken fern genus *Pteridium* Gled. ex Scop. (Dennstaedtiaceae) forms a readily delimited taxonomic entity (Tryon 1941; Cooper-Driver 1976:16) consistent with its probable origin through ancient allopolyploidy (Thomson 2000a, b). In contrast, infrageneric systematic treatment of the many morphotypes has proved extremely difficult, contentious and unstable. Factors contributing to this problem include phenotypic plasticity in relation to environmental variables, a dearth of useful taxonomic characters, and the widespread occurrence in the field of morphological intermediates between definable morphotypes (for references, see Thomson 2000a, b). These difficulties are exacerbated by inconsistencies in the application and/or definition of infraspecific taxonomic designations.

Within *Pteridium*, one major discontinuity stands out, allowing the diploid (based on 2n = 104) southern hemisphere brackens, *P. arachnoidenm* (Kaulf.) Maxon of C and S America and *P. esculentum* (G. Forst.) Cockayne, to be distinguished morphologically and genetically from the essentially northern hemisphere diploid bracken morphotypes of C and N America, Europe, Africa and Asia, that are currently placed collectively in *P. aquilinum* (L.) Kuhn (Thomson 2000a, b). This genetic discontinuity is reflected in the presence of the northern/southern allotetraploid (based on 4n = 208) species *P. candatum* (L.) Maxon in C and S America, and the analogous allotetraploid *P. semihastatum* (Wall. ex J. Agardh) S.B. Andrews (*P. yarrabeuse* (Domin) N.A. Wakef.) in South-East Asia/Australia (Thomson & Alonso-Amelot 2002).

Two problems are examined here in preparation for publication of several collaborative re-evaluations of the taxonomic status of bracken morphotypes from

C and N America, Europe, Africa and Asia. The first concerns controversy surrounding typification of *Pteridium aquilinum* (L.) Kuhn, a question central to taxonomic treatment of the whole genus. The second relates to current polemics on recognition of *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén as a pan-boreal taxon distributed from N America and northern Europe into north-east Asia (Karlsson 2000), versus treatment of the N European morphotype of this series as a distinct full species, *P. pinetorum* C.N. Page & R.R. Mill (Page & Mill 1995a, b; Page 1997; Hutchinson & Thomas 1996).

Towards an attempt to standardise infraspecific nomenclature in *Pteridium*, subspecies are here regarded as morphologically, biochemically and/or geographically distinct assemblages that are partially isolated genetically from other such assemblages, interbreeding between them being restricted to narrow contact zones. Varieties are here treated as distinct assemblages of populations that are morphologically, biochemically or geographically distinct, or only weakly distinct, with a greater area of overlap within which intermediate forms indicative of genetic exchange are encountered. Varieties may be grouped into subspecies that, in their totality, are significantly more distinct morphologically, biochemically and geographically (see Cronquist 1988). Increasing use in recent years of biochemical (including molecular) characters to supplement, or even in some cases to replace, morphology in these infraspecific contexts presents no logical difficulty. As Mabberley (2002:795) has written in another context: 'Should infrageneric groupings be recognised... such clades can, if necessary, be defined by molecular parameters, thereby obviating the need for botanists having to strive to find ever more obscure 'morphological features', which are ever more unusable for the layman trying to identify 'taxa' given names associated with ranks. There is, after all, no theoretical reason to suppose that all clades will be recognisable by eye, for evolution may act on chemical constitution, disease resistance etc., ...'

Typification of Pteridium aquilinum

Conflicting opinions concerning typification of Pteridium aquilinum (L.) Kuhn have recently been expressed in the literature, a problem of particular significance because of the central role of this taxon in structuring any systematic treatment of this cosmopolitan genus. Tryon's (1941) selection of Fuchs' 1542 illustration of Filix femina as the type for the basionym Pteris aquilina L. is explicit, even to consideration of the critical characters that it illustrates (Tryon 1941:18). Tardieu-Blot (1964) later named Hort. Cliff. 473, no. 6 (BM) as lectotype for this basionym without specifying whether she was referring to Hort. Cliff. 473, Pteris. 6? (since numbered BM000647565) or to Hort. Cliff. 473, Pteris 6 (now numbered BM000647566). Hort. Cliff. 473 Pteris 6? is, as noted by both Sheffield et al. (1989) and Page and Mill (1995b), typical of centralsouthern 'mid-latitude' European P. aquilinum subsp. aquilinum as currently understood. In contrast, Hort. Cliff. 473 Pteris 6 is labelled in Gronovius' hand 'Ex Nova Anglia attalit Dr Du Bois 5136' and is typical of P. aquilinum subsp. latiusculum (Desv.) Hultén from N America. As Linnaeus clearly states in the protologue for Pteris aquilina 'Habitat in Europae sylvis, praesertim caeduis', BM000647566 is ineligible, so Tardieu-Blot's (1964) choice must be taken as BM000647565. Subsequent to Tardieu-Blot's publication, Hort. Cliff. 473 Pteris 6? was labelled 'Lectotype of Pteris aquilina L. Determinavit B. Parris 12.2.1980' and regarded as such by Parris (1985:1884; B. Parris pers. comm. 2004) under ICBN rules pertaining before implementation of the Berlin Code of 1988. Presumably in view of introduction of the Berlin Code, Sheffield et al. (1989) in referring to Parris' annotation wrote: ' ... as far as we know no formal publication of this lectotypification has been made, and we do so here'. Page and Mill (1995b) commented in detail on, and supported, the action taken by Sheffield et al.

(1989). Bobrov's (1984:19) nomination of *Herb. Linn.* 1246.13 (LINN) as the type of *P. aquilinum* is superfluous and in any case inappropriate as this specimen is referable to subsp. *pinetorum* as defined below (see discussion in Page and Mill, 1995b:240), rather than to subsp. *aquilinum*.

Verdcourt (2000) recently re-examined the question of lectotypification of P. aquilinum. Although he describes Tardieu-Blot's (1964) selection as 'the more sensible choice', Verdcourt (2000:5) concluded that Tryon's choice of Fuchs' illustration is valid and must stand. S. Cafferty and C.E. Jarvis of the Linnaean Plant Name Typification Project (BM) concur with Verdcourt's opinion (S. Cafferty pers. comm. 2003), noting the absence of serious discrepancy between Tryon's selection and the protologue. Fuchs' plate provides little diagnostic detail; for instance it does not show nectaries at the pinna bases, and it is not clear from the outline drawing whether marginal sori are indicated or not. The illustration does, however, accord generally with Pteridinm aquilinum in regard to frond lamina proportions and cutting, presence of a false indusium and in rhizome features. Page and Mill (1995) comment that: 'The frond as drawn is slightly stunted and is typical of a P. aquiliuum plant growing in a somewhat dry place'. In view of the taxonomic complexities of , the availability of unequivocal type material of P. aquilinum (L.) Kuhn is particularly desirable. This end appears best reached by designation of Hort. Cliff. 473 Pteris 6? as epitype to support Fuchs' plate as the type of *P. aquilinum* as follows:

Pteridium aquilinum (L.) Kuhn in von der Decken, Reisen Ost Afrika 3(3):11 (1879).

Basionym: Pteris aquilina L., Species Plantarum 2:1075 (1753).

Type: [icon.] *Filix femina*, Fuchs, *Historiae Stirpium*: 596, misprinted 569 (1542), lectotype selected by Tryon (1941) [photograph seen, NSW].

Epitype: *Hortus Cliffortianus* 473 Pteris 6? (BM 000647565), selected here, [photograph seen, NSW].

Type locality: Europe.

Notes: Linnaeus' use of the specific name 'aquilina' for European bracken has been widely regarded as referring to the transitory eagle-like appearance of the apical pinnae during frond expansion (e.g. Page 1997:344). More likely, however, the name alluded to the widespread belief of Middle Age scholars (including Erasmus) and herbalists that the dark irregular outlines of the fibrovascular bundles evident in sections of bracken stipes and rhizomes symbolised either a double-headed eagle or an oak tree (Britten 1882). (Fig. 1).

The 'latiusculum' problem

Tryon's (1941) monograph established the concept that two principal bracken taxa, *P. aquilinum* var. *aquilinum* (his var. *typicum*) and *P. aquilinum* var. *latiusculum* (Desv.) Underw. ex A. Heller are represented in Europe, while in north-east Asia the two main taxa are, in Tryon's scheme, *P. aquilinum* var. *wightianum* (J. Agardh) R.M. Tryon and *P. aquilinum* var. *latiusculum*. The former is currently accorded subspecific rank as *P. aquilinum* subsp. *wightianum* (Wall. ex J. Agardh) W.C. Shieh, the latter as *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén with a pan-boreal distribution.

Subsequent to Page's (1989) identification of *P. aquilinum* subsp. *latiusculum* in Scotland, Page and Mill (1995a, b) controversially (see Rumsey et al. 1991) named the Scottish and continental European 'latiusculum' as a new full species, *P. pinetorum* C.N. Page and R.R. Mill. These authors also moved the 'latiusculum' morphotype *P. aquilinum* var. *osmundaceum* Christ into *P. pinetorum* as *P. pinetorum* subsp.

osmundaceum (Christ) C.N. Page. This treatment of northern European 'latiusculum' morphotypes has received wide coverage in British floras, most notably in *Welsh Ferus* (Hutchinson & Thomas 1996) and *The Ferus of Britain and Ireland* (Page 1997). More widely accepted, however, is the contrasting treatment of *Pteridium* in *Flora Nordica* (Karlsson 2000) that places all European brackens into either *P. aquilinum* subsp. *aquilinum* or *P. aquilinum* subsp. *latiusculum* and describes the scope of phenotypic variation within them.

Karlsson (2000) rejects Page's taxonomic treatment of European *Pteridium* in the following terms: 'However, there is no biological foundation for such a narrow species concept, and the distinctness of the N European plant (*P. pinetorum*) from the N American one (*P. latiusculum*) is not documented.' On the other hand, treatment of the 'latiusculum' morphotypes as comprising a single pan-boreal taxonomic entity, whether as a full species, *Pteridium latiusculum* (Desv.) Hieron. ex R.E. Fr., or as a subspecies, *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén, is also untenable in the light of recent morphological and molecular studies.

A number of lines of molecular evidence now support the conclusion that the N American, European and NE Asian 'latiusculum' morphotypes do not form a monophyletic assemblage, either overall or considered pairwise. This is consistent with morphological evidence of genetic exchange within each of these regions between the local 'latiusculum' and other morphotypes (Tryon 1941, Page 1989, Harmaja 1990, Karlsson 2000, Shorina & Perestoronina 2000).

These include:

(i) Isozyme analyses of 'aquilinum' morphotypes from Britain and 'latiusculum' morphotypes from Scotland (later ascribed to *P. pinetorum*), Denmark (Mon Island) and New Hampshire made by Rumsey et al. (1991) show that overall the 'latiusculum' plants are genetically more similar to each other than to the 'aquilinum' accessions tested. The European 'latiusculum' samples are more closely related to each other than to those from N America, and show isozyme patterns suggesting introgression from 'aquilinum'. These findings are consistent with the suggestion that the European and

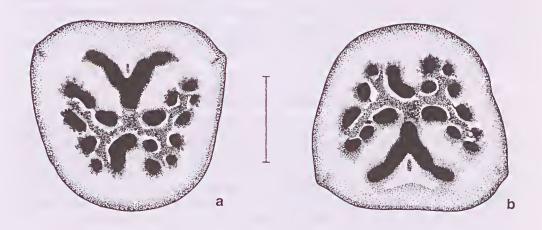


Fig. 1. *P. aquilinum* subsp. *aquilinum*, Wales UK. a,b, transverse sections of stipes close to their base, oriented to show patterns of fibrovascular bundles supposedly resembling a, double-headed eagle; b, oak tree; scale bar = 3 mm.

Table 1. Distribution of 455 rDNA restriction-site haplotypes in diploid morphotypes of *Pteridium*, compiled from data used by Thomson et al. (1995).

(¹estimated fragment lengths in kb; ²in parentheses: number of accessions/number examined)

Haplotype	Diagnostic restriction fragments ¹	Occurrence ²
А	Bgl II (7.9); Bst EII (7.5)	all morphotypes (23/23)
В	Bgl II (5.4 + 2.5); Bst EII (9.0); Bam HI (3.02 + 2.32 +1.70);	P. esculentum (3/3), P. arachnoideum (1/1)
С	Sac I (1.38 + 1.23) Bam HI (2.88 + 1.64)	NE Asian 'latiusculum' (4/4)
D	Sac I (1.55 + 1.41 + 1.17); probably also Bam HI (2.66)	P. aquilinum subsp. wightianum (4/4)
E	Sac I (1.46 + 1.25)	all N hemisphere morphotypes (15/15) except <i>P.</i> a <i>quilinum</i> subsp. <i>wightianum</i> (4/4)
F	Bam HI (2.24)	some European 'aquilinum' (2/5), some NE Asian 'latiusculum' (2/4), African 'aquilinum' (2/2), <i>P. aquilinum</i> subsp. <i>wightianum</i> (4/4), N American 'latiusculum' (1/1), European 'latiusculum' (1/1)

American 'latiusculum' morphotypes may not constitute a single taxon (Rumsey et al. 1991).

(ii) Comparative sequencing studies of the chloroplast genomes of N American and European brackens separate an 'aquilinum' clade from a '*latiusculum*' clade (Speer 2000), a finding in agreement with an earlier restriction site analysis (Wolf et al. 1995). Within the 'latiusculum' clade, accessions from Scotland (*P. pinetorum* subsp. *pinetorum* from its type locality), Sweden and Russia group more closely with each other than with N American samples, again suggesting genetic differentiation between the American and European forms, albeit at a level too low to warrant species-level treatment of either (Speer 2000).

(iii) Analysis of restriction endonuclease sites in the 45S rDNA sequences of bracken morphotypes (Thomson et al. 1995) leads to identification of six haplotypes (A-F, Table 1). Of these, haplotype A is found in all *Pteridium* taxa examined, together with haplotype B in *P. esculentum* and *P. araclmoideum*; with haplotypes C, E and/or F in NE Asian 'latiusculum'; with haplotypes D and F in *P. aquilinum* subsp. *wightianum*; with haplotypes E and F in 'latiusculum' from Europe (Ukraine) and N America; with haplotypes from E and/or F in other N American bracken taxa and in European *P. aquilinum* subsp. *aquilinum*. While these 45S rDNA haplotype patterns do not allow distinction between N American and European 'latiusculum', haplotype C is unique to NE Asian 'latiusculum'.

(iv) Phenetic clustering analysis of DNA-fingerprint band patterns of the nuclear genome of *Pteridium* taxa obtained using Arbitrarily-Primed (A-P) PCR (Thomson 2000a, b) groups NE Asian 'latiusculum' more closely with *P. aquilinum* var. *decompositum* (Gaudich.) R.M. Tryon from Hawaii than with N American 'latiusculum', while *P. pinetorum* clusters with European 'aquilinum' morphotypes.

Nomenclature of 'latiusculum' morphotypes

Given that treatment of 'latiusculum' morphotypes as a single pan-boreal taxonomic entity as currently understood (Karlsson 2000) is untenable (whether as a full species, *Pteridium latiusculum* (Desv.) Hieron. ex R.E. Fr., or as a subspecies, *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén), three regional subspecies are recognised here, restricted respectively to N America, Europe and Asia.

Pteridium aquilinum (L.) Kulm subsp. pinetorum (C.N. Page & R.R. Mill) J.A. Thomson, stat. nov.

Basionym: Pteridium pinetorum C.N. Page & R.R. Mill, Bot. J. Scotl. 47:140 (1994, publ. February 1995).

Type: C.N. Page 17049, Scotland, 4 June 1983, (holo: E 00026882 [seen]; iso: ABD, GL, PTH). Holotype cited by C.N. Page as voucher of *P. aquilinum* subsp. *latiusculum*, Watsonia 17:431 (1989).

Type locality: Scotland: East Inverness-shire, Rothiemurchus Forest near Loch an Eilein.

Synonymy: Pteridium aquilinum (L.) Kuhn var. osmundaceum Christ, Beitrage Krypt. Schweiz 1(2):54 (1900); Pteridium pinetorum C.N. Page & R.R. Mill subsp. osmundaceum (Christ) C.N. Page, Bot. J. Scotl. 47:140 (1994, publ. February 1995);

Pteridium aquilinum (L.) Kuhn var. *pinetorum* (C.N. Page & Mill) Perest. in N.I. Shorina and O.N. Perestoronina, Proc. Intl Bracken Group Conference, Manchester 1999, Bracken Fern: Toxicity, Biology and Control Ch. 7:51 (publ. August 2000).

Distribution: Restricted to N, C and E Europe, ranging from Scotland to Siberia, Scandinavia, Switzerland, Northern Italy and Northern Ukraine. Localities as for *P. aquilinum var. osmundaceum* (Christ 1900), *P. pinetorum* (Page & Mill 1995a, b; Hutchinson & Thomas 1996; Page 1997), *P. aquilinum* var. *pinetorum* in N and C Russia and Ukraine (Shorina & Perestoronina 2000) and *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén in Scandinavia (Karlsson 2000). Not in Crimea and the Caucasus Mountains (Shorina & Perestoronina 2000) or Armenia (Gabriěljan & Greuter 1984).

Chromosome complement (sporophyte): diploid, implied by the results of Rumsey et al. (1991); 2n = 104 (Sorsa 1961).

Notes: Christ's name 'osmundaceum' is not available at subspecific level in P. aquilinum under ICBN (Saint Louis Code) Art. 11.6. Nakai (1925) was aware that Christ (1900:54) had described a variety of P. aquilinum from Europe, but apparently he did not see the original description, and gives the following citation: 'Pteridium aquilinum var. osmundoides Christ apud Lévéille in Bull. Acad. Geogr. Bot. 3 ser. XIX. p.9 (1910), nihil aliud.' Tryon (1941, p. 23) lists this as a nomen nudum; var. osunundoides appears to be an erroneous reference to var. osmundaceum. Had Nakai had access to Christ's original (1900) paper, his comments might well have been interesting, and may have encouraged recognition of P. aquilinum var. osmundacenm in Europe, for he comments (Nakai 1925) that 'There are a few distinct varieties of Pteris aquilina (Pteridium aquilinum) in Europe. The variety from North Europe (including Up[p]sala) has similar lobes as var. osmundoides ...', and makes no reference to use of the name for Japanese material (Bonaparte 1918: 72, see below). For morphometric data on P. aquilinum in Eastern Europe see Shorina and Perestoronina (2000). Genetic analysis of populations in Scotland referred here to P. aquilinum subsp. pinetorum, has been reported by Bridges et al. (1998).

Pteridium aquilinum (L.) Kuhn subsp. japonicum (Nakai) Á. Löve & D. Löve, Taxon 26:325 (1977).

Basionym: Pteridium aquilimum (L.) Kuhn var. japonicum Nakai, Bot. Mag. (Tokyo) 39 (461):106 (1925).

Type: Torama Yoshinaga [s.n.], July 19th 1886, Pteris aquilina L. Pteridium aquilinum Kuhn [the latter identification in Nakai's handwriting], (lectotype selected here: TI [photographs seen, NSW]); syntypes designated here: C. Owatari s.n., 1 Nov. 1896, Keelung, Taiwan; K. Miyake s.n., 16 Oct. 1899, Taihoku, Taiwan; Nikai 720, 1910, Honshu, Japan; T. Nakai 4096, 31 May 1917, Korea; T. Nakai 6578, 28 Oct. 1917, Korea; T. Nakai 10460, 19 Jun. 1921, Korea; T. Nakai 10461, 28 Jun. 1921, Korea; (all TI [photographs seen, NSW]).

Type locality: Japan:Shimizu-toge, Echigo Province (now Niigata Prefecture), Honshu Island.

Synonymy: Pteridium japonicum (Nakai) Tardieu-Blot & C. Chr., Fl. Gen. Indo-Chine 7: 138 (1939–1951).

Distribution: The N E Asian region only, as specified for *P. aquilinum* var. *japonicum* by Nakai (1925), and as part of *P. aquilinum* var. *latinsculum* by Tryon (1941) and others, in Japan, Russia (Kamchatka, Amur, Sakhalin), Korea, China (extending west to Manchuria), Taiwan, North Vietnam, South Vietnam, Cambodia, Laos.

Chromosome complement (sporophyte): diploid, 2n =104 (Takahashi 1961, Kurita 1963).

Notes: Many sheets in TI carry the label *Pteridium aquilinum* var. *japonicum* Nakai in Professor Nakai's handwriting; none appears to have been so annotated before publication of this taxon in 1925 (H. Ohba, pers. comm. 2003). The lectotype is a well-spread, well-preserved, fertile frond from Japan, chosen from about 12 specimens in TI that can be identified as original material. A specimen from Sakhalin (*Père Urbain Faurie 304*, not seen) listed by Bonaparte (1918:72) as *P. aquilinum var. osmundaceum* Christ should presumably be referred to *P. aquilinum* subsp. *japonicum*.

Plants intermediate in morphology between *P. aquilinum* subsp. *japonicum* and *P. aquilinum* subsp. *wightianum* are well documented, particularly from China (e.g. Tryon 1941:44-5).

Pteridium aquilinum (L.) Kuhn subsp. **latiusculum** (Desv.) Hultén, *Lunds Univ. Arssk.* N.F. Avd 2, 37 no.1; 43 (1941) [*Flora of Alaska and Yukon*].

[Pteridium aquilinum (L.) Kuhn subsp. latiusculum (Desv.) Hultén ex R.T. Clausen, Cornell Univ. Agric. Exper. Stat. Mem. 291: 7 (1949)].

Basionym: Pteris latiuscula Desv., Mém. Soc. Linn. Paris 6(2): 303 (1827).

Type: 'Pteris latiuscula Desv.', Desvaux' Herbarium (holo: P 00347485); 'Pteris latiuscula Desv.' from de Vaillant's Herbarium (**new paratype:** P 00347522); 'Pt. caudata SCHK.' from the Herbarium of Danty d'Isnard (P00347486), (**new isoparatype**). [photographs seen, NSW].

Type locality: Canada: St. Pierre, Newfoundland.

Synonyms: *Pteridium latiusculum* Hieron. ex R.E. Fr., *Wiss. Erg. Schwed. Rhodesia-Kougo-Exped.* 1911–1912 1 : 7 (1914); *Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Desv.) Underw. ex A. Heller, *Cat. N. Am. Pl.*, 3 ed., 17 (1909); *Pteridium aquilinum* (L.) Kuhn subsp. *latiusculum* (Desv.) C.N.Page, *Watsonia* 17: 429,431 (1989).

Distribution: Circumscription of P. aquilinum (L.) Kuhn subsp. latiusculum (Desv.) amended here to include only specimens Hultén is from the N American region, encompassing plants from localities as specified for P. aquilinum var. latiusculum (Desv.) Underw. ex A. Heller by the following and other authors: Canada (Lellinger 1985, Cody & Britton 1989); USA (most abundantly in eastern and northern regions (Tryon 1941, Jacobs & Peck 1993, Lellinger 1985, Speer & Hilu 1999); Mexico (Nuevo Léon, Jacobs & Peck 1993).

Chromosome complement (sporophyte): diploid, 2n = 104 (Britton 1953, Cody & Mulligan 1982).

Notes: The original material for *Pteris latinscula* Desv. consists of three specimens in P. On P 000347485, the printed label 'HERB. MUS. PARIS' reads 'Herbier de A. N. DESVAUX Donné par Mme Vve LAVALLÉE en 1896' [Desvaux' initials N. A. presumably having been inadvertently transposed]. Other labels read 'Pteris Aquilina variété Occidentalis T. N et St. Pierre' [Terre Neuve = Newfoundland]; 'Pteris latiuscula Desv.' and 'Habitat in America boreali'. These annotations exactly match specifications in the protologue. P 00347522 ('Herbier de Vaillant') and P 00347486 ('Herbier de Danty d'Isnard') are both labelled 'Filix ramosa major ...' and 'No. 84 ex Canada' in the same hand and are evidently duplicates. P 00347522 carries in addition a bluish-coloured label 'espèce distincte, Pteris latiuscula Desv.' This specimen, sent to Vaillant in Paris during 1770 (Boivin 1977, 1978), was clearly used and probably annotated by Desvaux. P 00347486 is marked 'Pt. caudata SCHK.', which is listed as a synonym in the protologue for *Pteris latiuscula* Desv. It therefore appears appropriate to regard P 000347522 as a paratype and P 000347486 as an isoparatype of *Pteris latiuscula* Desv. (F. Rakotondrainibe (P), pers. comm. 2004).

The combination *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén (1941) was not accepted initially because Hultén made no reference to the basionym, leading Clausen (1949) to republish the combination. However, Hultén's combination is now considered valid under the ICBN (Saint Louis Code) Arts 33.2 and 33.3 (as it was published before 1 January 1953), rendering Clausen's later publication unnecessary. *P. aquilinum* subsp. *latiusculum* as defined in the present paper is genetically close to *P. aquilinum* subsp. *pseudocandatum* (Clute) Hultén (*P. aquilinum* var. *pseudocandatum* Clute) (Speer & Hilu 1999, Speer et al. 1999, Thomson 2000a, b), with which it hybridises at points of contact in the field (Speer et al. 1999).

Nomenclature of the endemic Hawaiian bracken fern

The endemic Hawaiian bracken morphotype, locally known as kïlau, has until recently been referred to *Pteridium aquilinum* var. *decompositum* (Gaudich.) R.M. Tryon, or to *P. decompositum* Gaudich. [nomen nudum] (Rumpf et al. 1994). A number of contemporary accounts of the fern flora of the Hawaiian Islands [e.g. Valier (1995), see also synonymy given by Palmer (2002)] have used the more appropriate rank *P. aquilinum* subsp. decompositum attributed to C.H. Lamoureux. This name, used in a draft list [Charles H. Lamoureux 1988, *Draft Checklist of Hawaiian Pteridophytes*, p.5] appears not to have been published before the untimely death of its author (C. Puttock, pers. comm. 2004), and is therefore formally published here.

Pteridium aquilinum (L.) Kulm subsp. decompositum (Gandich.) Lamoureux ex J.A. Thomson, stat. nov.

Basionym: Pteris decomposita Gaudich., Freyc. Voy. Bot. 393 (1829).

Type: '17. pteris Decomposita. iles Sandwich 1819: C. Gaudichaud' [sic] in Herb. Muséum d'Histoire Naturelle (holo: P 00347589, [photographs seen, NSW]).

Type locality: Hawaiian Islands.

Synonymy: *Pteridium capense* (Thunb.) Krasser var. *decompositum* (Gaudich.) Nakai, Bot. Mag. (Tokyo) 39 (461): 106 (1925); *Pteridium aquilinum var. decompositum* (Gaudich.) R.M. Tryon, Rhodora, 43: 40 (1941).

Distribution: Known only from the Hawaiian Islands (except Ni'ihau, Kaho'olawe).

Chromosome complement (sporophyte): diploid, 2n = 104 (Sheffield et al. 1995).

Notes: P00347589 is the only original material so far identified. Provenance of P00347587 'Gaudichaud Iles Sandwich' to the Herbarium of E. Drake (P) is uncertain; this sheet may have dated from either the Uranie or Bonite voyages. Gaudichaud himself collected P00347586, 'Voyage de M. Gaudichaud sur la Bonite. 1836-1837. Iles Sandwich. Septembre et Octobre, 1836' but this post-dated his description of *Pteris decomposita*. P00347588, O'Wai'he, M. Botta s.n., 1829 is also excluded by the date of collection.

DNA fingerprinting indicates that *P. aquiliuum* subsp. *decompositum* shares a unique combination of genomic elements otherwise found in subsp. *wightianum* and subsp. *japonicum* (Thomson, 2000a, b). Sequencing studies of the chloroplast genome suggest a close relationship with *P. aquiliuum* subsp. *lanuginosum* (Bong.) Hultén (*P. aquiliuum* var. *pubescens* Underw.) of western N America (Speer et al. 2002). Systematic crosses made by Klekowski (1973) have indicated that bracken from the Hawaiian Is. is intersterile with *P. arachnoideum* from the Galapagos Is., although at least partially fertile in crosses with certain S and C American accessions of *P. arachnoideum* and *P. caudatum*.

Acknowledgments

I thank Steve Cafferty and Charlie Jarvis (BM) for their assessment of the validity of Tryon's typification of P. aquilinum. Steve Cafferty kindly provided digital images of Fuch's plate of Pteris aquilina. Lesley Elkan provided the figure. Barbara Parris (Fern Research Foundation, Kerikeri) provided helpful comments on Hort. Cliff. sheets at BM. Roberta Cowan (ABLO, K), Harri Harmaja (H), Mitsuyasu Hasebe (National Institute for Basic Biology, Okazaki) and John Mickel (NY) supplied copies of reference materials not available in Australia. Goro Kokubugata (TNS) and Hideaki Ohba (TI) generously searched out and photographed specimens used by Takenoshin Nakai in describing P. aquilinum var. japonicum. I am further grateful to Hideaki Ohba for identifying Professor Nakai's handwriting, and for comments on the selection of the lectotype for this taxon, and I thank the Director of TI for access to this material. 1 thank the Director of P for access to material described by Desvaux and by Gaudichaud, and I am deeply indebted to France Rakotondrainibe (P) for taxonomic advice, historical references, and digital imaging of this material. I greatly appreciate the help of Christopher Puttock (BISH) in tracking down unpublished work on taxonomy of Hawaiian bracken, and with pleasure join him in paying tribute to the botanical and cultural contribution of Charlie Lamoureux (b. 1933, d. 2000), Professor of Botany, University of Hawai'i (HAW), and Director of the Harold L. Lyon Arboretum in Mänoa. I acknowledge many helpful comments and suggestions received from colleagues at NSW, including Elizabeth Brown, Barbara Briggs, Carrick Chambers, Joy Everett, David Mabberley, Chris Quinn, Peter Weston, Karen Wilson and Peter Wilson. Mary Gunson's comments and criticisms of an earlier draft greatly improved the manuscript.

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Manuscript received 30 Jan 2004 Manuscript accepted 1 July 2004

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